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Habitat Partitioning by Two Sympatric Species of Chipmunk (Genus: *Neotamias*) in the Warner Mountains of California

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Abstract.—In the Warner Mountains of California, two sympatric species of chipmunk partition their habitat primarily through the mechanism of competitive exclusion by social dominance and aggressive interactions. Forests are optimal habitats for both *Neotamias amoenus* and *N. minimus*. In this study *N. amoenus* actively excludes *N. minimus* from the forest through successful aggressive interspecific interactions, leaving N. *minimus* to occupy primarily the arid sagebrush scrub. *Neotamias amoenus* was observed to be the more social species. *Neotamias minimus* appears to lack the level of social structure of *N. amoenus* and was not observed to win any aggressive encounters. *Neotamias minimus* avoids interaction with *N. amoenus*.

It is generally accepted that two species cannot occupy the same area, utilizing the same resources during the same time (Savage 1958; Whittaker et al. 1973). The question then arises as to how can two or more closely related species occupy the same locality. Competitive exclusion is a mechanism that has been proposed to explain the utilization of the same area by two similar species (Brown 1971; Connell 1961). Competitive exclusion is the exclusion of one species by another from mutually desirable resources (Armstrong and McGehee 1980). One species can exclude another from a resource through a variety of mechanisms that may include social and physical dominance. Although dominance is usually discussed within a particular species, the same principles can apply to interspecific interactions between morphologically similar species (Morse 1974).

Chipmunks (genus *Neotamias*) are ecologically diverse rodents that can be found in a wide array of habitats across North America. Most species are contiguously allopatric and actively partition common habitat areas (Heller 1971). A number of species may share a relatively small area, but distributions tend only to be abutting with overlapping ranges kept to a minimum (Patterson 1980). Chipmunks achieve nearly non-overlapping ranges through various mechanisms of competitive exclusion such as aggression (Brown 1971; Chappel 1978; Meredith 1976; Sheppard 1971) and avoidance (Morse 1974; Sheppard 1971). The importance of interspecific dominance, as a mechanism of habitat partitioning, through interspecific aggression between chipmunk species has been supported and well documented by Brown (1971), Chappell (1978) Heller (1971), Meredith (1976), Sheppard (1971), and others. For example, it has been documented that in a laboratory setting *N. amoenus* is dominant over *N. minimus* through aggressive interactions (Sheppard 1971; Meredith 1976).

Neotamias minimus is the most widely distributed of all North American chipmunks and occupies a wide spectrum of habitats such as sagebrush scrub, woodland, and alpine

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scrub (Sheppard 1971, Hall 1981, Bergstrom 1992, Verts & Carraway 2001). *Neotamias amoenus*, although less widespread than *N. minimus*, can be found abundantly throughout open brush and dense forests in the Pacific Northwest, Idaho, Montana, and Wyoming (Hall 1981, Sheppard 1971, Meredith 1976, Sutton 1992). In the Warner Mountains of northeastern California, *N. amoenus* can be found primarily in the conifer forests, while *N. minimus* predominately occupies the sagebrush scrub, with both species being abundant in an intermediate ecotonal area containing a relatively even mixture of conifers and sagebrush. It was in this overlapping intermediate area that a unique opportunity was available to observe frequent interspecific interactions between these two species and to test the hypothesis of competitive exclusion through aggressive dominance by *N. amoenus*.

This study addressed the question of how *N. amoenus* and *N. minimus* partition their habitat in the Warner Mountains, Modoc County, California. Based on the results of previous studies (Brown 1971, Chappell 1978, Heller 1971, Meredith 1976, and Sheppard 1971) it is hypothesized that competitive exclusion through interspecific aggression and avoidance may be the mechanisms by which these two species partition their habitat.

Materials and Methods

Study Site

All data were collected from a single site in the Warner Mountains, Modoc National Forest, Modoc County, California. The site was located approximately 13 km East of Blue Lake Campground at an elevation of 2105 meters above sea level (N 41° 11′, W 120° 14′).

The study site consisted of three habitats: coniferous forest, sagebrush scrub, and an area of ecotone between the two. The conifer forest community is an area dominated by lodgepole pine (*Pinus contorta*), Jeffrey pine (*Pinus jeffreyi*), and white fir (*Abies concolor*). Ground cover consisted of grasses, forbs, mule ears (*Wyethia helenioides*), yellow bush lupine (*Lupinus arboreus*) and indian paintbrush (*Castilleja coccinea*). The sagebrush scrub community contained mostly big sagebrush (*Artemisia tridentata*) with only a few scattered conifers. The intermediate (ecotonal) community was defined as an area with a mixture of both big sagebrush and conifers.

Species Identification

Although these two chipmunks closely resemble one another, they are distinguishable on the basis of several characteristics. *Neotamias minimus* has an average total length of 167–225 mm, average tail length of 70–114 mm, and an average weight of 32–50 g (Verts and Carraway 2001). *Neotamias amoenus* has an average total body length of 186–238 mm, average tail length of 72–109 mm, and an average body weight of 36–50 g (Sutton 1992). In this study (N = 179), *N. amoenus* and *N. minimus* ranged in actual observed weight from 39–59 g (n = 117) and 31–56 g (n = 62), respectively.

The major differences that make them distinguishable in the field are that *N. minimus* is generally smaller and paler than *N. amoenus* with the fur located on the underside of the tail being more yellowish, the rostrum being shorter, and having a tawny tuft of fur at the base of the ear. *Neotamias amoenus* is in turn distinguishable from *N. minimus* by not having the above features and having a more reddish under-tail and broader, lighter dorsal stripes (Hall, 1981; Kays and Wilson, 2002). Male and female individuals could not be distinguished in the field.

Habitat Utilization

Chipmunk utilization of the three habitats was determined by live trapping. One hundred folding aluminum Sherman live traps (7.6 × 9.0 × 23.4 cm) with galvanized steel doors were placed in a 190 × 90 m grid. The grid consisted of ten trap-lines placed 20 m apart with ten traps per line set 10 m apart. The grid was oriented so that the trap-lines ran northeast to southwest. Each of the four corners was marked with an aluminum stake for the duration of the study. Each of the 100 traps was flagged and sequentially numbered (1 to 100) starting in the forest. The grid was placed so that each habitat type was sampled. The conifer forest and sagebrush scrub contained three trap lines each, while the ecotone area contained four (Figure 1).

A total of thirteen days of trapping was conducted (three each in July and September, and seven in August). Traps were baited using a combination of oats, dried fruit, raw almonds, and raw sunflower seeds. Traps were set at 0700 hrs and checked and closed by 1000 hrs. Captured animals were identified to species and gender, ear tagged with a numbered monel small animal ear tag and weighed. Any significant conditions such as obvious pregnancy, lactation, or scrotal distention were recorded. The animals were then released.

Behavioral Interactions

Artificial feeding stations (similar to those described by Brown 1971) were utilized to observe possible interspecific and intraspecific interactions. Feeding stations consisted of a small food pile located in an area where both species were known to occur and that had an unobstructed view. Dried fruits, raw almonds, raw sunflower seeds, and uncooked oats were used to attract visitors to the feeding station. A total of four feeding stations was established, one each in the coniferous forest and sagebrush scrub and two in the ecotone.

Observations were conducted from observation areas approximately 10 m from the feeding stations. A Winchester spotting scope (15–45 × 50 mm), Bushnell 10 × 25 mm compact binoculars, Olympus handheld micro-cassette recorder, and Olympus Camedia C-750 digital camera were used to assist in the collection of data.

A Sony Digital 8 Camcorder was used to record ninety-minute spans of continuous real time data of chipmunk interactions while at the feeding station. These included feeding, grooming, social, and aggressive behaviors. All observed behaviors and interactions, both interspecific and intraspecific, were recorded along with the respective times and dates.

An aggressive interaction was defined as an event between two or more individuals of the same or different species that included biting, chasing, vocalization directed at a specific individual, or fighting. An individual was deemed a winner of the aggressive interaction if that individual was successful in defending its position. The individual who abandoned the position was deemed the loser of the event. An event where an individual made a clear and distinct attempt to travel towards a feeding station but was halted by the presence of another individual or group and then clearly changed course was considered an avoidance interaction.

Although the distance (10 m) between the observation areas and the feeding stations was relatively close this was the maximum distance that allowed the two species to be easily distinguished. To verify that this distance did not have an effect on the subjects, the number of visits to the feeding station while under human observation ($n = 39$) were

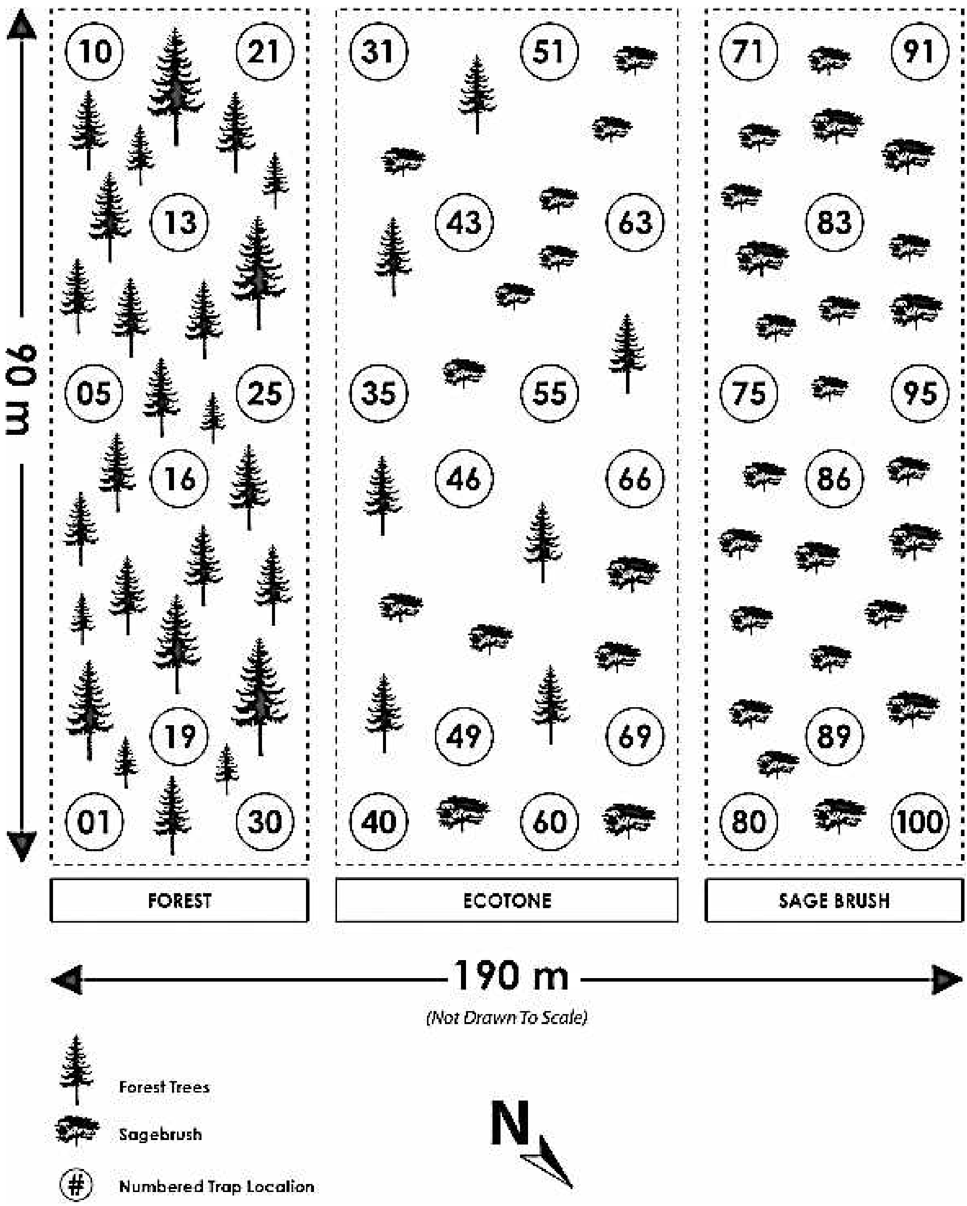

Fig. 1. Schematic map of the study area showing selected trapping stations, approximate distribution of major vegetation, and the layout of "forest", "ecotone", and "sagebrush scrub" habitats (map not drawn to scale).

compared to the number of visits to the feeding station under video monitoring (n = 31). There was no significant difference between the two ($X^2 = 0.914$, 1 df, $p \geq 0.339$).

All fieldwork and handling of animals was conducted under Animal Protocol #793 approved by the San Jose State University Institutional Animal Care and Use Committee and California Department of Fish and Game scientific collecting permit (#SC-007372) following the guidelines of the American Society of Mammalogists (Animal Care and Use

Table 1. Chi Square Goodness of Fit for chipmunk habitat utilization.

	N. amoenus Captured	*N. minimus* Captured	df	X^2	P
Forest	84	10	1	58.24	< 0.001
Ecotone	28	25	1	0.17	> 0.05
Sagebrush	5	27	1	15.12	< 0.001

Committee 1998). Six voucher specimens (three of each species) were preserved as vouchers and deposited in the Bird and Mammal collections at San Jose State University (*N. minimus* #'s 3524-3526 and *N. amoenus* #'s 3527-3529).

Results

Habitat Utilization

A total of 1300 trap-days yielded 179 captures (Table 1). Both *N. amoenus* and *N. minimus* were abundant in the study area with 65% of captures consisting of *N. amoenus* and 35% of captures consisting of *N. minimus*. Males were more readily captured than females and 52% of the sample was recaptures. Trapping effort was most successful in the forest area, Traps 1–30 (Figure 1), with 52% of the captures. The ecotone and sagebrush areas accounted for 30% and 18% of the captures, respectively. In the forest area, *N. amoenus* was the most abundant, comprising 89% of the sample (Table 1). There was no significant difference (Table 1) in the distribution of these two species in the ecotone area (Traps 31–70, Figure 1). In the sagebrush area (Traps 71–100, Figure 1), *N. minimus* was the species most caught and consisted of 84% of the captures (Table 1).

Behavioral Interactions

A total of 80 interspecific interactions between *N. amoenus* and *N. minimus* was recorded at the artificial feeding stations (Table 2). Of the 80 total interactions, 65% were aggressive with *N. amoenus* clearly the physical aggressor, while the remaining 35% were avoidance behaviors taken by *N. minimus* in response to the aggression by *N. amoenus* (Table 2).

Discussion

Habitat Utilization

It is evident that, at this site, *N. amoenus* and *N. minimus* occupy distinct habitat types (Table 1). In the conifer dominated areas the most abundant species was *N. amoenus*, with a small number of *N. minimus*. In the arid sagebrush areas, *N. minimus* was the most abundant. In the ecotonal area there was no significant difference in the numbers of *N. amoenus* and *N. minimus* (Table 1). These data support the conclusion that *N. amoenus* appears to be excluding *N. minimus* from the forest, as was reported by Sheppard (1971). Chappell (1978) suggests that it is the ability of *N. minimus* to tolerate a higher heat load and lower water loss that allows it to live in less than optimal conditions. Therefore, the

Table 2. Chi Square Test for Independence for chipmunk interspecific interactions.

	N. amoenus	*N. minimus*	df	X^2	P
Aggressive Interactions Won	52	0	1	75.69	< 0.001
Interactions Avoided	0	28			

conditions of the arid sagebrush may be excluding *N. amoenus* or may be helping to restrict *N. minimus*.

Behavioral Interactions

The artificial feeding stations were highly successful in attracting both species at the same times during the day. The most successful station was located in an ecotonal area easily accessible to both species. Once both species began utilizing the feeding stations a clear hierarchy was established both intra- and interspecifically. *Neotamias amoenus* proved to be the more aggressive and social species of the two (Table 2).

Many intraspecific aggressive interactions were observed between *N. amoenus* individuals at the feeding stations. There were times when some individuals would feed in a group and other times where a dominant *N. amoenus* would chase off conspecifics and feed alone. *Neotamias amoenus* was frequently observed traveling in groups of two to four individuals. Other animals would visit the feeding stations from time to time including golden mantle ground squirrels (*Spermophilus lateralis*) and Steller's jay (*Cyanocitta stelleri*). These animals would either share the station with chipmunks or chase away a single or pair of chipmunks. However, if there was a group of at least three *N. amoenus*, then *N. amoenus* would be successful in chasing away other animals taking control of the feeding station. This observation demonstrates the advantage to *N. amoenus* of not only being aggressive (Chappell 1978; Meredith 1976; Sheppard 1971) but, also, to travel in social groups.

Neotamias minimus visited the feeding stations far less often than *N. amoenus*. *Neotamias minimus* appears to be a solitary species and was never observed approaching a feeding station in groups. Only when there were no other animals within close proximity (at least 5 m) of the feeding station did an individual *N. minimus* approach the station. This species also showed no obvious signs of intra- or interspecific aggression throughout the study. Avoidance, the act of an individual changing course or direction in response to the presence of an individual of the opposing species (Sheppard 1971), was a commonly observed behavior in *N. minimus* and accounted for 35% of the total behavioral observations (Table 2). In every avoidance encounter recorded, *N. minimus* would change course or direction apparently to avoid *N. amoenus*.

Conclusion

From data presented in this study it appears that *N. amoenus* excludes *N. minimus* from the forest area through the competitive exclusion mechanisms of social dominance and aggressive interactions. Although it is suggested in this study and by previous studies that both species are capable of existing in all three habitats (forest, ecotone, sagebrush scrub), *N. amoenus* tends to primarily occupy the forest while *N. minimus* occupies mostly sagebrush scrub. Observations in this study confirm that *N. amoenus* is the more aggressive species and that it is a more social animal than *N. minimus*. These two traits seem to confer a competitive advantage to *N. amoenus* allowing it to occupy its preferred habitat and exclude *N. minimus. Neotamias minimus* was not observed to have won any aggressive bouts with *N. amoenus* and appears to lack the social structure seen in *N. amoenus*. *Neotamias minimus* was always observed traveling and feeding alone, whereas, *N. amoenus* was observed, at times, to travel and feed in small social groups. These important life history aspects, aggression by *N. amoenus* and avoidance by *N. minimus,* have led, most likely, to the current habitat partitioning between these two species observed in this study.

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